# A diverse Eocene fish scale assemblage from Seymour Island, Antarctica

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#### ABSTRACT

A collection of fish scales from the La Meseta Formation (Paleogene, Eocene; Seymour Island, Antarctica) has been studied, permitting the characterisation of five clearly distinguishable morphotypes. Three morphotypes are comparable to scales of recent trachichthyids, clupeids, and gadids. The other two morphotypes are represented only by two poorly preserved specimens; however, they probably pertain to perciform and pleuronectiform fishes. The latter is a new record for the La Meseta Formation. The mixed composition of the fish scale assemblage reflects substantial redistribution of fish remains within a high-energy, shallow marine environment. Scales were recovered from calcareous sandstone concretions, which accounts for their overall good preservation. This is the most diversified assemblage of fish scales yet reported from the fossil record of Antarctica.

## RÉSUMÉ

Un assemblage diversifié d'écailles de poissons en provenance de l'Île Seymour, Antarctique. Une collection d'écailles de poissons en provenance de la Formation de La Meseta (Paléogène, Éocène; Île Seymour, Antarctique) a été étudiée, permettant la caractérisation de cinq morphotypes clairement différenciés. Trois sont comparables aux écailles actuelles des trachichthyidés, des clupéidés et des gadidés. Les deux autres morphotypes sont représentés uniquement par deux spécimens mal conservés; cependant, ils appartiennent probablement à des poissons

KEY WORDS Teleostei, scales, lepidology, Eocene, La Meseta Formation, Antarctica. MOTS CLÉS Teleostei, écailles, lépidologie, Éocene, Formation de La Meseta, Antarctique. perciformes ou pleuronectiformes. Le pleuronectiforme correspond à un nouveau signalement pour la Formation de La Meseta. La composition mixte de cet assemblage d'écailles de poissons est le reflet d'une redistribution substantielle des restes de poissons à l'intérieur d'un milieu marin à haute énergie. Les écailles ont été retrouvées dans des concrétions calcaires gréseuses, ce qui a permis leur assez bonne conservation. C'est l'assemblage d'écailles fossiles de poissons le plus diversifié de l'Antarctique.

## INTRODUCTION

The Eocene La Meseta Formation has provided a rich record of elasmobranchian and teleostean material, which was been described by many authors during last few decades (e.g., Grande & Eastman 1986; Jerzmańska 1991; Cione *et al.* 1994; Kriwet & Hecht 2008; and many others).

The first mention of the presence of teleost fossils in Tertiary deposits of Seymour Island was by Woodward (1908). He described isolated vertebrae which he assigned to genus Notothenia Richardson, 1844 (the determination is highly tentative; see also discussion in Grande & Eastman 1986). Currently, actinopterygian fish remains from Eocene deposits are assigned to the following groups of teleosts: Gadiformes (Jerzmańska 1988; Eastman & Grande 1991; Jerzmańska & Świdnicki 1992; Doktor et al. 1996), Macrouridae Gilbert & Hubbs, 1916 (Kriwet & Hecht 2008), Clupeidae Bonaparte, 1831 (Jerzmańska 1991; Doktor et al. 1996), Siluriformes (Grande & Eastman 1986), Eleginopsidae Gill, 1862 (Balushkin 1994), Trichiuridae Rafinesque, 1810 (Long 1991), Labridae Cuvier, 1816 (Long 1992), Oplegnathidae Bleeker, 1854 (Cione et al. 1994), Beryciformes (Doktor et al. 1996), and Xiphiorhynchinae Regan, 1909 (Cione et al. 2001). Specimens consist mainly of isolated skeletal elements, although several articulated remains are known.

Information on fossil fish scales within this material is quite limited, and, when mentioned at all, is usually very brief (Grande & Eastman 1986: 131; or Mesozoic beryciform scales mentioned by Grande & Chatterjee 1987: 835, fig. 3). By contrast, Jerzmańska (1991) and Doktor *et al.* (1996) provided detailed description of isolated scales.

Scales may be used to decode life-history variables, such as age (e.g., Rifflart *et al.* 2006; Osipov & Kiyashko 2008) and size (e.g., Duncan 1980), but they also may be used for taxonomic determinations. Fossil and subrecent scales can be utilized to yield this kind of information as well (David 1956; Patterson *et al.* 2002; Wright *et al.* 2005), although problems of diagenetic alteration, morphological variability and lack of recent analogs may complicate interpretation.

The main aims of this study are: 1) to describe a new collection of Eocene fossil fish scales from La Meseta Formation; 2) to delimit several morphotypes within the collection, and to compare them to their probable recent equivalents; and 3) finally, to assess their use as indicators of paleoenvironment.

## GEOLOGICAL SETTINGS

The Jurassic-Cenozoic sedimentary succession of the James Ross Island area has been interpreted as a small part of a large sedimentary basin, originally defined as the Larsen Basin (Macdonald *et al.* 1988). Elliot (1988) used the term James Ross Basin for the Mesozoic-Tertiary sequence in the James Ross Island area (Fig. 1). The James Ross Basin represents one of the principal Late Mesozoic-early Cenozoic back-arc basins now exposed within Peninsula-Scotia arc region (palaeolatitude 60-65°S). The basin-fill comprises an approximately 6-km-thick succession of arc-derived volcaniclastic sedimentary rocks which have been subdivided formally into



FIG. 1. — Maps of the studied area: **A**, schematic map showing the location of James Ross Island region; **B**, detail of Gustav, Marambio and Seymour Island Groups of the James Ross Island region; based on Crame & Luther (1997); **C**, major stratigraphic units on Seymour Island with positions of localities yielding fish scales indicated (this study), based on Sadler (1988). For coordinates and stratigraphic position of samples see Material and methods section and Figure 2.

three lithostratigraphical groups: the Lower-Upper Cretaceous Gustav Group, the Upper Cretaceouslowermost Tertiary Marambio Group, and the lower Tertiary Seymour Island Group (Figs 1, 2; Ineson *et al.* 1986; Pirrie 1991; Crame *et al.* 1991; Pirrie *et al.* 1997; Crame & Luther 1997).

The youngest strata within the James Ross Basin comprise the Early-Late Eocene La Meseta Formation, which crops out on Seymour (Rinaldi *et al.* 1978; Elliot & Trautman 1982) and Cockburn islands (Askin *et al.* 1991). On northern Seymour Island, approximately 750 m of Eocene La Meseta Formation, a shallow-water marine deposit consisting of muddy sands with minor sandstones and coquinas, overlie the early Paleogene Cross Valley and Sobral formations and Late Cretaceous López de Bertodano Formation consisting of mudstones and sands (Figs 1, 2; Elliot & Trautman 1982; Macellari 1988; Sadler 1988; Pirrie 1991; Elliot *et al.* 1992; Dingle *et al.* 1998; Marenssi *et al.* 1998).

Predominantly marine-estuarine sediments of the La Meseta Formation were deposited from the Early Eocene (Ypresian, 49.5 Ma) low stand of sea level (Sadler 1988), to the latest Eocene (34.2 Ma), according to Sr isotope dating (Dingle & Lavelle 1998) and dinoflagellates (Wrenn & Hart 1988; Cocozza & Clarke 1992). The base of the La Meseta Formation is marked by a prominent unconformity, with considerable erosional relief (Sadler 1988; Pirrie et al. 1992). The La Meseta Formation is 750-800 m thick (Rinaldi et al. 1978; Elliot 1988; Stilwell & Zinsmeister 1992) and exhibits largescale coarsening-upward cycles from mudstones to sandstones, with laterally complex shell beds at the top of the cycles. Sadler (1988) demonstrated that these sediments show the geometry of incisedshelf valleys and mapped the formation in terms of seven disconformity-based units, Telm 1 to Telm 7 (Fig. 2). Results of subsequent research suggest that the La Meseta Formation can be subdivided into



FIG. 2. — Stratigraphic position of teleost fish remains within the La Meseta Formation. Based on references in Geological Settings section; stratigraphic position of localities with fish scales indicated by star (this study). For geographical location see Material and methods section and Figure 1.

six (Marenssi 1995; Marenssi et al. 1998; Marenssi 2006) or seven (Porebski 1995) units that represent fluctuating base level changes (Porebski 2000). In places these sediments are very rich in marine and terrestrial fossils (Feldmann & Woodburne 1988; Stilwell & Zinsmeister 1992), concentrated often in shell conglomerates lithified by calcareous cement. Dingle et al. (1998) based the paleoclimate interpretation of the late Cretaceous to Eocene strata on Seymour Island on mineralogical, sedimentological and geochemical climatic proxies; these data show that the northern Antarctic Peninsula (Seymour Island, La Meseta Formation) experienced a climatic deterioration from very warm, non-seasonally wet conditions at the end of the Palaeogene global optimum (early Middle Eocene c. 47 Ma) to a latest Eocene (post *c*. 34 Ma) regime that was cold, frostprone and relatively dry (Dingle *et al.* 1998). The La Meseta Formation is overlain by post-Pliocene glacial deposits of the Weddell Formation (Fig. 1; Zinsmeister & de Vries 1983; Gaździcki *et al.* 1999).

# MATERIAL AND METHODS

All specimens were collected during the 2008 and 2010 expeditions of the Czech Geological Survey at locality N3 (64°13'17.8"S, 56°36'51.3"W) and a nearby locality N7 (64°13'16.6"S, 56°37'08.9"W) within La Meseta Formation, northern Seymour Island, Antarctica (Fig. 1). Sediments of both localities show identical lithology and faunal content (see Faunal Assemblage and Taphonomy section) and are therefore suggested to be contemporaneous.

The 45 specimens were studied from locality N3 (N3/S1-N3/S45) and 28 specimens from locality N7 (N7/S46-N7/S73). All figured and studied material, thin sections and accompanying macrofauna, are housed in collections of the Czech Geological Survey, Prague.

Almost all specimens were left unprepared, excluding specimen N7/S64, which was prepared by thin (mechanical) needle under binocular microscope.

# TERMINOLOGY

Terminology for scale features mainly follows Lagler (1947). Furthermore, we used the terms primary, secondary and tertiary circuli, for different circuli generations. All characters used for scale description are figured (Fig. 3). As has been mentioned by many authors, scale shape is not the best taxonomic indicator (Chikuni 1968; Casteel 1973; Patterson *et al.* 2002), and in our analyses we used broader morphological evaluations. We accept the usage of the term "spinoid scale" (Roberts 1993).

# FAUNAL ASSEMBLAGE AND TAPHONOMY

Fish scales and other numerous and well-preserved fauna and flora were found within intensively lithified ball-like to irregular calcareous sandstone concretions



FIG. 3. — Morphological features used for description of studied specimens. Terminology mainly follows Lagler (1947): **A**, schematized clupeid scale (cycloid type); **B**, schematized gadid scale (cycloid type); **C**, schematized ctenoid (spinoid) scale. For description of morphological features see Material and methods section and Lagler (1947).



Fig. 4. — Teleostei fish scales with associated macrofauna from locality N3 (La Meseta Fm., Seymour Island): **A**, fish scale (morphotype 1) in a fragment of calcareous concretion associated with shells of invertebrates and coalified plant remains; specimen N3/S45; **B**, thin section of calcareous sandstone concretion with fish scale (morphotype 4) exhibiting densely packed macrofaunal and plant remains; thin section N3/C4/R1. Abbreviations: **Bi**, bivalve; **Br**, bryozoan; **E**, echinoderm; **G**, gastropod; **P**, coalified plant remain; **S**, fish scale. Scale bars: 2 mm.

weathering out from poorly lithified silty sands. These sediments correspond to the lower part of unit Telm 3 sensu Sadler (1988) and to the upper part of the Acantilados allomember (Marenssi et al. 1998) (Fig. 2). Fish scales within calcareous concretions are abundant, typically associated with prolific and diversified macrofaunal and plant remains (Fig. 4). Invertebrates are represented mainly by mollusks – especially bivalves (*Cockburnia* Zinsmeister, 1984; *Periploma* Schumacher, 1817; *Panopea* Menard, 1807; *Modiolus* Lamarck, 1799; *Mactra* Linnaeus, 1767; *Solemya* Lamarck, 1818; and *Nucula* Lamarck, 1799) and gastropods (Naticidae Guilding, 1834; Buccinidae Rafinesque, 1815; Muricidae da Costa, 1776; Struthiolariidae Gabb, 1868; Cerithidae Fleming, 1822). There is striking presence of both juvenile and adult shells of nautilids (*Euciphoceras argentinae* [del Valle *et al.*, 1976]) suggesting transport and/or immigration from their normal deep habitat (for discussion of analogous occurrences see Zinsmeister 1987 and Dzik & Gaździcki 2001). Noteworthy also is the presence of fragmentary preserved echinoid tests and bryozoan colonies (Fig. 4). Plant remains are represented by: 1) abundant and well-preserved *Nothofagus* Blume leaves; 2) three-dimensionally preserved leafy branches of araucarian conifers; and



FiG. 5. – Scale morphotype 1, Eocene, Seymour Island, Antarctica; cf. Beryciformes, family Trachichthyidae: **A**, specimen N7/S49; **B**<sub>1</sub>, specimen N3/S39; **B**<sub>2</sub>, detail of specimen N3/S39, border between primary and secondary circuli; **C**, specimen N3/S16; **D**<sub>1</sub>, specimen N7/S47, inner side of the scale. Dotted line shows ctenoid field, arrow shows roughened area; **D**<sub>2</sub>, specimen N7/S47, detail of the roughened area; **E**, specimen N3/S9; **F**, specimen N7/S50, arrows show prominent spines; **G**, specimen N7/S64; **H**, reconstruction of the morphotype 1. Scale bars: A, D<sub>1</sub>, H, 2 mm; B<sub>1</sub>, C, E, F, 1 mm; B<sub>2</sub>, D<sub>2</sub>, 500 µm; G, 3 mm

3) calcified/coalified angiosperm and conifer wood. Wood occurs both in small fragments and larger log fragments containing occasional borings of *Teredolites* Leymerie, 1842 filled by geopetal sediment.

Taphonomy of the accompanying macrofauna and macroflora (e.g., well preserved and often articulated bivalves, three-dimensionally preserved branches of araucarian conifers) and faunal and floral composition suggest rapid burial and early diagenetic origin of calcareous sandstone concretions. The presence of terrestrial plants, shallowwater and deep-water invertebrates suggests mixing of fauna and flora in fully marine, but shallow water conditions.

## DESCRIPTION

The studied specimens were separated into five easily distinguishable morphotypic groups:

## MORPHOTYPE 1 (FIG. 5)

Ctenoid scales with subsquarish shape. In some cases, the shape is suboval (specimen N3/S17) to



FiG. 6. – Scale morphotype 2, Eocene, Seymour Island, Antarctica; possible Pleuronectiformes: **A**, specimen N3/S30a; **B**<sub>1</sub>, specimen N7/S46; **B**<sub>2</sub>, detail of specimen N7/S46, ctenoid field, turned position; **C**, reconstruction of morphotype 2. Scale bars: A, 1 mm; B<sub>1</sub>, 5 mm; B<sub>2</sub>, 500 µm; C, 3 mm.

irregular (specimen N7/S50). The scales are typical spinoid. The cranial edge is convex with a more anteriorly prominent medial portion; the caudal margin is slightly rounded to triangular in shape. Focus is relatively large and deep, and lies in the longitudal axis of the scale. No radii are marked. Two to three different generations of circuli (margin between two generations is marked by arrow in Fig. 5B<sub>2</sub>) may be recognised.

The ctenoid field is diamond shaped, without circuli, and in some cases is caudally elongated (e.g., N7/S71). The ctenii are spinelike, in several alternating rows (Fig. 5A) and some markedly project from the scale (e.g., N7/S51, N7/S50, marked by arrows in Fig. 5F). On the larger scales (e.g., N7/S70) ctenii are generally finer, but also more numerous. Ctenii closer to the nucleus are smaller than those in the peripheral part of the scale (N7/S67).

Two specimens show remnants of a large spine (or elevation) in the longitudinal axis of the scale. The base of one such large elevation is preserved on specimen N7/S64 (Fig. 5G). Another large elevation is preserved on the specimen N7/S66 in negative impression.

On the inner surface of the scale, the posterior field is diamond shaped (dotted line in Fig.  $5D_1$ ); in the middle of the posterior field there is a rough area (marked by arrow in Fig.  $5D_1$ , detail in  $5D_2$ ).

Estimated maximal antero-posterior length is about 13 mm (based on specimen N7/S70); maximal depth is about 15 mm (based on specimen N3/S45). Ratio of length to depth is not constant because of the variable shape of individual scales.

Specimens N3/S9 (Fig. 5E), S28, S33, S34, S40 and N7/S62 are generally similar to those described above, but the ctenoid field is naked (morphosubtype 1.1). Specimen N3/S26 presents one part of the posterior field covered by ctenii and the other part naked; also specimen N3/S2 has about ¼ of the posterior field naked. These specimens represent the transition from the type 1 to the subtype 1.1.

Specimens N3/S16 and S35 show naked posterior fields, but the posterior margin is sculptured by several small ridges (Fig. 5C).

Specimens: N3/S1-3, N3/S8-S11, N3/S16, N3/ S17, N3/S26-S28, N3/S32-S35, N3/S39, N3/S40, N3/S45, N7/S47-S51, N7/S61, N7/S62, N7/ S64-S67, N7/S70, N7/S71 (32 specimens without counterparts).

#### MORPHOTYPE 2 (FIG. 6)

The shape of this scale is slightly asymmetrical, suboval. Focus is large and antero-posteriorly elongated. Ctenoid field is prolate, without prominent spines. Ctenii are wave-shaped, but are preserved



FiG. 7. — Scale morphotype 3, Eocene, Seymour Island, Antarctica; probably Perciformes: **A**<sub>1</sub>, specimen N7/S57; **A**<sub>2</sub>, detail of specimen N7/S57, imprint of ctenoid field; **A**<sub>3</sub>, detail of specimen N7/S57, different generation of circuli; **B**, reconstruction of morphotype 3. Scale bars: A<sub>1</sub>, 1 mm; A<sub>2</sub>, A<sub>3</sub>, 500 μm; B, 2 mm.

only as broken bases and are therefore incomplete. Detailed description is not possible.

In the central area of specimen N7/S46 (Fig. 6B) the material of the scale is missing, thus exposing the imprint of the granulated sculpture of its inner surface. At the cranial margin, there is preserved a single indentation, from which runs a radius, partly preserved in scale material, partly just as an imprint. The imprint of a second radius is also present. The ctenoid field is not sufficiently preserved for description (see detail in Fig. 6B<sub>2</sub>). Estimated antero-posterior length is about 25 mm; estimated depth is about 18 mm.

A smaller specimen (N3/S30, Fig. 6A) has an elongated focus, with eight preserved radii. It is also possible to recognise primary and secondary circuli on the lateral field. The ctenoid field and cranial margin are missing.

Specimens: N3/S30, N7/S46 (two specimens without counterparts).

## Morphotype 3 (Fig. 7)

The shape of these scales is subquadrilateral. There are numerous fine circuli; on the lateral field it is possible to recognise three generations (Fig. 7A<sub>3</sub>): primary, secondary, and tertiary. The focus is shifted to the posterior half of the scale. From the anterior margin (which is not preserved in our material) there are 4 to 6 radii running towards the focus. The posterior (ctenoid) field has a dorsoventrally elongated diamond shape. Isolated ctenii are not visible, just a system of fanlike folds (with centers close to the focus). Folds are represented in relatively high number (about 50) and probably represent imprints of ctenii series (Fig. 7A<sub>2</sub>).

Specimens: N3/S12 and N7/S57 (two specimens without counterparts).

#### MORPHOTYPE 4 (FIG. 8)

Roundish scales, cycloid to subquadrilateral in shape, typically with transverse striae. The posterior part of the scale is convex, with an elevated middle part, and its surface lacks perforations, but has discrete longitudinal striations (Fig. 8D).

The circuli are extremely fine. The posteriormost stria is continuous and runs through the nucleus; in some cases scales are broken at the level of the continuous striae. It is possible to recognise two groups within morphotype 4, which are distinguishable on the basis of the size and number of



FIG. 8. — Scale morphotype 4, Eocene, Seymour Island, Antarctica; family Clupeidae (**B-E**, genus and species indet.): **A**, specimen N3/S7, referred to *Marambionella andreae*; **B**, specimen N3/S31; **C**, specimen N7/S68; **D**, specimen N3/S24, isolated posterior field of the scale; **E**, specimen N7/S53; **F**, reconstruction of morphotype 4. Scale bars: A, C, 2 mm; B, E, 5 mm; D, F, 1 mm.

striae situated anteriorly from the posteriormost (continuous) stria:

The first group is represented by smaller type (diameter about 7-8 mm, maximally 10 mm), with 4-5 developed interrupted striae (e.g., specimen N3/S7, Fig. 8A).

The second type is larger, with diameter from 10 to 16 mm. There are 6 to 9 interrupted striae developed (e.g., specimens N7/S53, Fig. 8E and N7/S68, Fig. 8C).

Several specimens (e.g., N3/S37 and N3/S38) lack organized striae. In specimen N3/S5 the posterior field is fully developed while the anterior part is feebly developed, with one small stria.

Specimens: N3/S5-S7, N3/S14, N3/S15, N3/ S18-S25, N3/S31, N3/S36-S38, N3/S43, N7/ S52-S55, N7/S58-S60, N7/S63, N7/S68, N7/S69 (28 specimens without counterparts).

## MORPHOTYPE 5 (FIG. 9)

Elongated oval cycloid scales with numerous circuli. Axis of elongation lies in the middle of the scale and



FIG. 9. — Scale morphotype 5, Eocene, Seymour Island, Antarctica; identified as Gadiformes, cf. Merlucciidae: A, specimen N7/S72; B, reconstruction of morphotype 5. Scale bars: A, 1 mm; B, 2 mm.

runs through the nucleus. Circuli are fused together at an acute angle in the posterior field (Fig. 9A). The posterior field is longer than the anterior field. No radii are visible. Specimens: N3/S4, N3/S13, N3/S41, N3/S42, N3/S44, N7/S72, N7/S73 (7 specimens without counterparts).

# DISCUSSION

All teleost groups described from skeletal remains within Eocene sediments of La Meseta Formation have developed scales, except members of order Siluriformes and family Trichiuridae (Bruton 1996; Nakamura & Parin 1993, respectively).

On the basis of morphological description and comparison with data concerning scale morphology of recent fishes, it is possible to assign the specimens reviewed here to these taxonomic groups:

## MORPHOTYPE 1 (FIG. 5)

These typically spinoid scales can probably be referred to the family Trachichthyidae Cuvier, 1829 (order Beryciformes). This interpretation is supported by the presence of a large ctenoid field without marked circuli, with distinct spines in several alternating rows and lack of radii. Such scales were figured and described by Gon (1987) and Nakae & Sasaki (2002). The rough area on the inner surface of the scale (specimen N7/S47) could possibly represent a scale regeneration.

It should be mentioned that scales described by Doktor *et al.* (1996) as resembling those of trachichthyids are not same as the specimens studied herein, for the following reasons: the scales previously described are markedly smaller; the shape of spines is different (spines are relatively short with broad base, see figure 13 in Doktor *et al.* 1996); and the numerous circuli are parallel to the lateral edges of the scale. On the other hand, it is necessary to consider the possibility of ontogenetic variability.

Specimens with entirely naked ctenoid fields (e.g., N3/S28, N3/S33, N3/S34) represent a morphologically extreme case. Several specimens (e.g., N3/S26) were recovered that display a continual transition from the type showing an extremity with spines (ctenii) to types with naked ctenoid fields. This large morphological variability is probably due to scales from a different body region, ontogeny, or sexual dimorphism. No trachichthyid skeletal remains from the Eocene sediments have been described, although some are known from the Cretaceous sediments of Antarctica (Grande & Chatterjee 1987).

The recent trachichthyids are marine with a depth distribution of about 100-1500 m and many species are characteristic of deep water environments (Nelson 2006).

A few scales of morphotype 1 are also similar to those of order Gadiformes, family Macrouridae, but differ in lacking circuli within the ctenoid field. This feature was pointed out by Marshall & Iwamoto (1973, *non vidi*), Cohen *et al.* (1990) and Nakae & Sasaki (2002). It is necessary to point out that, on specimens N3/S16 (Fig. 5C) and N3/S35, very feebly developed circuli are found within the caudal field, and the posterior margin is sculpted by several ridges. Thus it is possible that these specimens have closer affinity to the macrourids rather than to the trachichthyids.

The possible presence of macrourid scales could be expected as macrourid skeletal remains are known from Eocene sediments of the La Meseta Formation (Kriwet & Hecht 2008).

Most macrourids are benthopelagic marine fishes with depth distribution of 200-2000 m (Nelson 2006).

# MORPHOTYPE 2 (FIG. 6)

The scales are classified into separate group because of their clearly different morphological character, although insufficiently preserved features do not allow stringent assignment to any specific taxonomic group. On the other hand, the large focus area and presence of typical bases of numerous ctenii (Fig. 6B<sub>2</sub>) may indicate possible affinity to Pleuronectiformes (Patterson *et al.* 2002: some specimens in figs 48, 49, 54-57). This taxon has not previously been reported from the La Meseta Formation.

# Morphotype 3 (Fig. 7)

The scales of this type are tentatively assigned to the ctenoid type. In the posterior field a series of ridges is developed, which probably represent the imprint of the ctenii series. The posterior edge is not preserved so little can be said about characters of the ctenii. Three generations of circuli are distinguishable in the lateral fields (Fig.  $7A_3$ ). The scales probably pertain to perciforms. Insufficient preservation of characteristic features does not allow a more precise determination.

# Morphotype 4 (Fig. 8)

These cycloid scales clearly pertain to clupeids. The clupeid *Marambionella andreae* Jerzmańska, 1991 from Paleogene sediments of La Meseta Formation (Jerzmańska 1991) has been described on the basis of the skeletal material with which scales were associated.

As mentioned above, it is possible to divide the specimens studied herein into two groups: the first group could be assigned to *Marambionella andreae* (rounded, relatively thick cycloid scales with continuous posteriormost stria and with 4 to 5 anteriorly interrupted striae according to Jerzmańska 1991; Fig. 8A). The second group differs from *M. andreae* in the higher number of interrupted striae and different size (Fig. 8C, E).

It is well known that intraspecfic variability of the clupeid scale is extreme and depends on individual development and place of developmental origin (fossil examples were figured by Sato 1966: fig. 5; Szymczyk 1978: fig. 4). For this reason it is difficult to determine if the slightly different morphology represents individual variability, origin from a different region of the fish body, or scales of entirely different taxa.

Recent clupeids are primarily marine fishes living in shoals near the surface (Whitehead 1985; Nelson 2006).

# Morphotype 5 (Fig. 9)

The cycloid scales of this type are easily recognizable and it is possible to assign them to gadiforms, probably family Merlucciidae Gill, 1844 (Fig. 5). Although similar scales were also described by Doktor *et al.* (1996), our specimens differ from them in being larger and in expressing a more acute angle of the circuli in the posterior field (20-25° as opposed to 30°). A similar type of scale has been figured by many authors from different stratigraphic levels and geographic locations (Novitskaia 1961: fig. 2; Fedotov 1976: figs 5a, **6**; Patterson *et al.* 2002: figs 23.1-23.12).

We are not in agreement with Kriwet & Hecht (2008) that the scales described by Doktor *et al.* 

(1996) as gadids probably pertain to clupeids. They differ from the latter in having an elongated shape, marked circuli, the angle of circuli in the posterior field, and in lacking transverse striae.

The presence of gadid fish within La Meseta Formation is also well supported by the presence of skeletal remains (Jerzmańska 1988; Jerzmańska & Świdnicki 1992). In the posterior field of specimen N7/S72 the shape of the circuli is disturbed. This part of the scale probably represents a healed injury or regeneration.

Today, living merlucciids inhabit the continental shelf and upper slope, but some enter estuaries and/or deep water – more than 1000 m (Cohen *et al.* 1990).

# GENERAL NOTES

Some groups described on the basis of skeletal records, such as oplegnathids, labrids, and possible notothenioids (depends on interpretation; see Eastman & Grande 1991 and Balushkin 1994), have specific scale types that are more or less easily distinguishable. Unfortunately, such scales were not found in the studied collection.

From the paleoecological point of view, the fish assemblage is represented mainly by neritic clupeids with deep water forms (trachichthyids) and several specimens of other taxa with clearly different ecological demands. The salinity conditions are not paleoecologically clearly distinguishable, but the presence of typical marine elements reflects a fully marine environment (see also Geological Settings and Faunal Assemblage and Taphonomy sections). On the other hand it should be mentioned that the fossil assemblage does not represent a natural biotic composition but consists of taphonomically sorted material brought together from perhaps several marine habitats.

# CONCLUSIONS

The first large collection of fossil fish scales from the Antarctica is described. Five separate morphotypes are defined, described and briefly discussed with probable taxonomic determination. Taphonomic data suggest that the taxa represented lived in a fully marine environment with continental influence, relatively close to the coast.

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# REFERENCES

- ASKIN R. A., ELLIOT D. H., STILWELL J. D. & ZINSMEIS-TER W. J. 1991. — Stratigraphy and paleontology of Campanian and Eocene sediments, Cockburn Island, Antarctic Peninsula. *Journal of South American Earth Sciences* 4: 99-117.
- BALUSHKIN A. V. 1994. Proeleginops grandeastmanorum gen. et sp. nov. (Perciformes, Notothenioidei, Eleginopsidae) from the Late Eocene of Seymour Island (Antarctica) is a fossil notothenioid, not a gadiform. Journal of Ichthyology 34: 10-23.
- BRUTON M. N. 1996. Alternative life-history strategies of catfishes. *Aquatic Living Resources* 9: 35-41.
- CASTEEL R. W. 1973. The scales of the native freshwater fish families of Washington. *Northwest Science* 47: 230-238.
- CHIKUNI S. 1968. On the scale characters of the Pacific Ocean perch in the Bering Sea. I. Some scale characters and their variations by body regions. *Bulletin of the Japanese Society of Scientific Fisheries* 34: 681-686.
- CIONE A. L., AZPELICUETA M. M. & BELLWOOD D. R. 1994. — An oplegnathid fish from the Eocene of Antarctica. *Palaeontology* 37: 931-940.
- CIONE A. L., REGUERO M. A. & ELLIOTT D. H. 2001. A large osteichthyan vertebra from the Eocene of Antarctica. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 2001: 543-552.

- COCOZZA C. D. & CLARKE C. M. 1992. Eocene microplankton from La Meseta Formation, northern Seymour Island. *Antarctic Science* 4: 355-362.
- COHEN M. D., INADA T., IWAMOTO T. & SCIALABBA, N. 1990. — Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. *FAO species catalogue. Vol. 10. FAO Fisheries Synopsis No. 125* 10: 1-442.
- CRAME J. A., PIRRIE D., RIDING J. B. & THOMSON M. R. A. 1991. — Campanian-Maastrichtian (Cretaceous) stratigraphy of the James Ross Island area, Antarctica. *Journal of the Geological Society of London* 148: 1125-1140.
- CRAME J. A. & LUTHER A. 1997. The last inoceramid bivalves in Antarctica. *Cretaceous Research* 18: 179-195.
- DAVID L. R. 1956. Tertiary Anacanthin Fishes from California and the Pacific Northwest; Their Paleoecological Significance. *Journal of Paleontology* 30: 568-607.
- DINGLE R. V. & LAVELLE M. 1998. Late Cretaceous-Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141: 79-101.
- DINGLE R. V., MARENSSI S. A. & LAVELLE M. 1998. High latitude Eocene climate deterioration: evidence from the northern Antarctic Peninsula. *Journal of South American Earth Sciences* 11: 571-579.
- DOKTOR M., GAŹDZICKI A., JERZMAŃSKA A., PORĘBSKI S. J. & ZASTAWNIAK E. 1996. — A plant and fish assemblage from the Eocene La Meseta Formation of Seymour Island (Antarctic Peninsula) and its environmental implications. *Palaeontologia Polonica* 55: 127-146.
- DUNCAN K. W. 1980. On the back-calculation of fish lengths; modifications and extensions to the Fraser-Lee equation. *Journal of Fish Biology* 16: 725-730.
- DZIK J. & GAŹDZICKI A. 2001. The Eocene expansion of nautiloids to high latitudes. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 172: 297-312.
- EASTMAN J. T. & GRANDE L. 1991. Late Eocene gadiform (Teleostei) skull from Seymour Island, Antarctic Peninsula. *Antarctic Science* 3: 87-95.
- ELLIOT D. H. 1988. Tectonic setting and evolution of the James Ross Basin, northern Antarctic Peninsula. *Geological Society of America Memoir* 169: 541-555.
- ELLIOT D. H. & TRAUTMAN T. 1982. Lower Tertiary strata on Seymour Island, Antarctic Peninsula, *in* CRADDOCK C. (ed.), *Antarctic Geoscience*. University of Wisconsin Press, Madison: 287-297.
- ELLIOT D. H., HOFFMAN S. M. & RIESKE D. E. 1992. Provenance of Paleocene strata, Seymour Island, *in* YOSHIDA Y., KAMINUMA K. & SHIRAISHI K. (eds), *Recent progress in Antarctic Earth Science*. Terra Scientific Publishing Company, Tokyo: 347-355.

- FEDOTOV V. F. 1976. Treskovye paleogen-neogenovych otloženij SSSR [The Gadidae of the Paleogene-Neogene from the USSR]. Nauka, Moscow, 83 p.
- FELDMANN R. M. & WOODBURNE M. O. 1988. Geology and paleontology of Seymour Island, Antarctic Peninsula. *Geological Society of America Memoir* 169: 1-566.
- GAŹDZICKI A., TATUR A. & DEL VALLE R. 1999. The Weddell Formation: post Late Pliocene glacial deposits on Seymour Island, Antarctic Peninsula, *in* SKINNER D. N. B. (ed.), 8<sup>th</sup> International Symposium on Antarctic Earth Sciences: programme and abstracts. Victoria University of Wellington, Wellington: 117.
- GON O. 1987. New records of three fish species from Hawaii. Japanese Journal of Ichthyology 34: 100-104.
- GRANDE L. & EASTMAN J. T. 1986. A review of Antarctic ichthyofaunas in the light of new fossil discoveries. *Palaeontology* 29: 113-137.
- GRANDE L. & CHATTERJEE S. 1987. New Cretaceous fish fossils from Seymour Island, Antarctic Peninsula. *Palaeontology* 30: 829-837.
- INESON J. R., CRAME J. A. & THOMSON M. R. A. 1986. Lithostratigraphy of the Cretaceous strata of west James Ross Island. *Cretaceous Research* 7: 141-159.
- JERZMAŃSKA A. 1988. Isolated vertebrae of teleostean fishes from the Paleogene of Antarctica. *Polish Polar Research* 9: 421-435.
- JERZMAŃSKA A. 1991. First articulated teleost fish from the Paleogene of West Antarctica. *Antarctic Science* 3: 309-316.
- JERZMAŃSKA A. & ŚWIDNICKI J. 1992. Gadiform remains from the La Meseta Formation (Eocene) of Seymour Island, West Antarctica. *Polish Polar Research* 13: 241-253.
- KRIWET J. & HECHT T. 2008. A review of early gadiform evolution and diversification: first record of a rattail fish skull (Gadiformes, Macrouridae) from the Eocene of Antarctica, with otoliths preserved in situ. *Naturwissenschaften* 95: 899-907.
- LAGLER K. F. 1947. Lepidological Studies 1. Scale Characters of the Families of Great Lakes Fishes. *Transactions of the American Microscopical Society* 66: 149-171.
- LONG D. J. 1991. Fossil cutlassfish (Perciformes: Trichiuridae) teeth from the La Meseta Formation (Eocene), Seymour Island, Antarctic Peninsula. *PaleoBios* 13: 3-6.
- LONG D. J. 1992. An Eocene wrasse (Perciformes; Labridae) from Seymour Island. *Antarctic Science* 4: 235-237
- MACDONALD D. I. M., BARKER P. F., GARRETT S. W., INESON J. R., PIRRIE D., STOREY B. C., WHITHAM A. G., KINGHORN R. R. F. & MARSHALL J. E. A. 1988. — A preliminary assessment of the hydrocarbon potential of the Larsen Basin: Antarctica. *Marine and Petroleum Geology* 5: 34-53.

- MACELLARI C. E. 1988. Stratigraphy, sedimentology, and paleoecology of Upper Cretaceous/Paleocene shelf-deltaic sediments of Seymour Island. *Geological Society of America Memoir* 169: 25-53.
- MARENSSI S. A. 1995. Sedimentología y paleoambientes de sedimentació de la Formación La Meseta, isla Marambio, Antártida, Parts I & II. PhD thesis (unpublished). University of Buenos Aires, Buenos Aires, 330 p.
- MARENSSI S. Å. 2006. Eustatically controlled sedimentation recorded by Eocene strata of the James Ross Basin, Antarctica, Cretaceous-Tertiary High-Latitude Palaeoenvironments: James Ross Basin Antarctica. *The Geological Society of London, Special Publications* 258: 125-133.
- MARENSSI S. A., SANTILLANA S. N. & RINALDI C. A. 1998. — Stratigraphy of the La Meseta Formation (Eocene), Marambio (Seymour) Island, Antarctica. *Asociacion Paleontologica Argentina, Publication Especial* 5: 137-146.
- MARSHALL N. B. & IWAMOTO T. 1973. Family Macrouridae, excepting genera *Coelorhynchus*, *Coryphaenoides*, *Hymenocephalus* and *Nezumia*, *in* COHEN D. M. (ed.), *Fishes of the western North Atlantic, Part six*. Sears Foundation of Marine Research Memoirs, New Haven: 496-665.
- NAKAE M. & SASAKI K. 2002. A scale-eating triacanthodid, *Macrorhamphosodes uradoi*: prey fishes and mouth "handedness" (Tetraodontiformes, Triacanthoidei). *Ichthyological Research* 49: 7-14.
- NAKAMURA I. & PARIN N. V. 1993. Snake mackerels and cutlassfishes of the world (families Gempylidae and Trichiuridae). FAO species catalogue. Vol. 15. FAO Fisheries Synopsis No. 125 15: 1-136.
- NELSON J. S. 2006. Fishes of the World (4<sup>th</sup> edition). John Wiley & Sons, Inc., Hoboken, 601 p.
- NOVITSKAYA L. I. 1961. Rod *Palaeogadus* (Gadidae) is hadumskogo gorisonta Kavkasa [Genus *Palaeogadus* (Gadidae) from the Khadumian Horizon of Caucasus]. *Paleontologičeskij žurnal* 4: 120-130.
- OSIPOV V. V. & KIYASHKO V. I. 2008. Method of Age Determination of Ponto-Caspian Kilka *Clupeonella cultriventris* (Clupeiformes, Clupeoidei) Using Scales and Otoliths. *Journal of Ichthyology* 48: 637-643.
- PATTERSON R. T., WRIGHT C., CHANG A. S., TAYLOR L. A., LYONS P. D., DALLIMORE A. & KUMAR A. 2002. — Atlas of common squamatological (fish scale) material in coastal British Columbia, and an assessment of the utility of various scale types in paleofisheries reconstruction. *Palaeontologia Electronica* 4: 1-88.
- PIRRIE D. 1991. Controls on the petrographic evolution of an active margin sedimentary sequence: the Larsen Basin, Antarctica. *The Geological Society of London Special Publication* 57: 231-249.
- PIRRIE D., DUANE A. M. & RIDING J. B. 1992. Jurassic-Tertiary stratigraphy and palynology of the

James Ross Basin: review and introduction. *Antarctic Science* 4: 259-266.

- PIRRIE D., CRAME J. A., LOMAS S. A. & RIDING J. B. 1997. — Late Cretaceous lithostratigraphy and palynology of the Admirality Sound region, James Ross Basin, Antarctica. *Cretaceous Research* 18: 109-137.
- PORĘBSKI S. J. 1995. Facies architecture in a tectonically-controlled incised-valley estuary: La Meseta Formation (Eocene) of Seymour Island, Antarctic Peninsula. *Studia Geologica Polonica* 107: 7-97.
- PORĘBSKI S. J. 2000. Shelf-valley compound fill produced by fault subsidence and eustatic sea-level changes, Eocene La Meseta Formation, Seymour Island, Antarctica. *Geology* 28: 147-150.
- RIFFLART R., MARCHAND F., RIVOT E. & BAGLINIERE J.-L. 2006. — Scale reading validation for estimating age from tagged fish recapture in a brown trout (*Salmo trutta*) population. *Fisheries Research* 78: 380-384.
- RINALDI C. Å., MASSABIE A., MORELLI J., ROSENMAN H. L. & DEL VALLE R. 1978. — Geologia de la isla Vicecomodoro Marambio. *Contribuciones Científicas del Instituto Antárctico Argentino* 217: 5-43.
- ROBERTS C. D. 1993. Comparative Morphology of Spined Scales and their Phylogenetic Significance in the Teleostei. *Bulletin of Marine Science* 52: 60-113.
- SADLER P. M. 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. *Geological Society of America Memoir* 169: 303-320.
- SATO J. 1966. A new genus and species of sardine from the Miocene Hishinai Formation, north-eastern Japan. *Japanese Journal of Ichthyology* 13: 112-125.

- STILWELL J. D. & ZINSMEISTER W. J. 1992. Molluscan systematics and biostratigraphy. Lower Tertiary La Meseta Formation, Seymour Island, Antarctic Peninsula. *Antarctic Research Series* 55: 1-192.
- SZYMCZYK W. 1978. Clupeid scales from the Menilite Beds (Palaeogene) of the Carpathians. *Acta Palaeontologica Polonica* 23: 387-407.
- WHITEHEAD P. J. P. 1985. Clupeoid fishes of the world (suborder Clupeioidei). An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1 – Chirocentridae, Clupeidae and Pristigasteridae. FAO Species Catalogue. Vol. 7. FAO Fisheries Synopsis 1257: 1-303.
- WOODWARD A. S. 1908. On fossil Fish-Remains from Snow Hill and Seymour Islands. Wissenschaftliche Ergebnisse der schwedischen Südpolar-Expedition 1901-1903 3: 1-4.
- WRENN J. H. & HART G. F. 1988. Paleogene dinoflagellate cyst biostratigraphy of Seymour Island, Antarctica. *Geological Society of America Memoir* 169: 321-447.
- WRIGHT C. A., DALLIMORE A., THOMSON R. E., PAT-TERSON R. T. & WARE D. 2005. — Late Holocene paleofish populations in Effingham Inlet, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology* 224: 367-384.
- ZINSMEISTER W. J. 1987. Unusual nautilid occurrence in the Upper Eocene La Meseta Formation, Seymour Island, Antarctica. *Journal of Paleontology* 61: 724-726.
- ZINSMEISTER W. J. & DE VRIES T. J. 1983. Quaternary glacial marine deposits on Seymour Island. *Antarctic Journal of United States* 18: 64-65.

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